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ON TRIPLE HYBRIDS

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Twin hybrids are produced when the pollen of *Oenothera Lamarckiana* or of one of its derivatives is crossed with the European subspecies of *O. biennis* or of *O. muricata*. These twins appear in about equal numbers and are constant in succeeding generations. One of them, *O. laeta*, is broad and smooth leaved; the other, *O. velutina*, is more hairy and has furrow-shaped leaves.[1]

Triple hybrids may be produced by combining this phenomenon with the hereditary qualities of *O. lata* and *O. scintillans*. Both of them originated in my garden from *O. Lamarckiana*. *O. lata* is female, its anthers are barren. *O. scintillans* is an inconstant species which repeats its type only in one-third or two-thirds of its offspring. Both of them, when pollinated by *O. Lamarckiana*, give a mixed progeny, only part of which is like the mother.[2]

In order to get triplets, therefore, we have to cross *O. lata* or *O. scintillans* with some species which will split them into *laeta* and *velutina* (as it would do *O. Lamarckiana* itself or some others of its mutant species), and which, moreover, does not prevent them from repeating their own type in their progeny. The triplets will then be *O. laeta*, *O. velutina*, and *O. lata*. The first two will drop the special character of the mutant-parent (BOT. GAZ. *l. c.* 403), but all three will be intermediate hybrids between *O. Lamarckiana* or *O. lata* and the species used as the other parent.

I found that *O. strigosa* Rydberg, *O. Hookeri* T. and G., and the common American subspecies of *O. biennis* L. comply with these requirements. The experiments to be described in this article are limited to the effects of their pollen on *O. lata* and *O. scintillans*.

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[1] BOT. GAZETTE 44:401–407. 1907.

[2] *Die Mutations-Theorie.* Vols. I and II.

O. strigosa Rydb. has very small flowers, of the size of those of *O. muricata*, but in less dense spikes. They open their anthers two or more days before unfolding the corolla, and the pollen comes in contact with the whole outer surface of the stigma and causes fertilization. The leaves are bluish green and furrow-shaped, and the tip is bent sideways. The tops of young shoots, when seen from above, therefore, present the aspect of a wheel with spokes all curved to the left or to the right. This striking feature is repeated, though somewhat reduced, in all of its hybrids and causes them to be easily recognized. I collected seed in the Yellowstone Park in 1904. Another lot was kindly sent to me by Mr. T. D. A. COCKERELL from Boulder, Colorado. Of both strains I have since cultivated two generations.

In crossing *O. strigosa* with *O. Lamarckiana*, twins arise which combine the characters of *laeta* and *velutina* with those of *strigosa*. They differ more widely from one another than do the twins of any other cross I have studied up to this time. The *velutina* is almost like the *velutina* of *O. muricata* × *Lamarckiana*, but has the bluish tinge, the more pointed leaves with bent tips, and the wheel-shaped tops of the young shoots described above for *O. strigosa*. The *laeta* from the *strigosa* cross is a very stout plant with very broad leaves (6^{cm}), blunt at the apex and indented at the base, with smooth surface, and bright green. The flower buds are more narrowly conical than those of *velutina*, the flowers open more widely, the fruits are conical with four sharp and protruding teeth, whereas those of *velutina* are blunt and short. By this mark and by the somewhat narrowed neck of the fruits of *velutina*, the two forms are most easily distinguished when flowering is over. The *laeta* is usually poor, but the *velutina* is rich in pollen.

In contrast to the species previously dealt with, *O. strigosa* produces twins from *O. Lamarckiana* when used as male parent as well as when used as female parent. In these reciprocal crosses both of the twins are identical.

The twins produced by *O. strigosa* from *O. scintillans* and from *O. lata* comply with the description given. They cannot be distinguished from them externally, even when cultivated in large and pure lots.

O. Hookeri T. and G. is a Californian species and is also found in Texas.[3] I collected seeds in the vicinity of Berkeley, California, and another lot was sent to me from Riverside by Mr. FRED M. REED. It is a striking species, even more beautiful than *O. Lamarckiana.* The flowers are of the same size, protruding their pistils high above the anthers; but the petals are more deeply emarginate at the tip, nearly obcordate, and a paler yellow. The plant is hairy and reddish, and the leaves (especially those of the rosette) are long and narrow.

With *Lamarckiana* it produces twins identical in both reciprocal crosses and both of them as large-flowered as the parent species. The *laeta* is bright green, with smooth leaves and slender flower buds. The *velutina* is hairy and reddish, with furrow-shaped leaves and thick buds. It flowers more profusely and resembles *O. Hookeri* almost exactly, but is stouter, with dense and richly flowered spikes.

The twins derived by *O. Hookeri* from *O. lata* cannot be distinguished externally from those derived from *O. Lamarckiana.*

The American subspecies of *O. biennis* used for my experiments was collected by me in 1904 at Chicago, near Jackson Park. It seems to be the same form as that which is most common in the eastern states. Other subspecies I have collected in Pennsylvania, Kansas, Missouri, and elsewhere. All of them are quite different from the European form, which is the one used in my *Mutations-Theorie* and in my article on twin hybrids (BOT. GAZETTE *l. c.*). A systematic treatment of these numerous forms is still wanting, and therefore I will provisionally designate my strain by the name of its source and call it *Chicago.* Its most curious quality is that of producing twins when combined as a male parent with *O. Lamarckiana* and not when crossed with the pollen of this species. In this respect it is exactly opposite to the European *O. biennis,* and therefore very useful.

The *O. biennis* from Chicago is a taller plant, more richly branched, and darker green than the European form. Its flowers are much smaller, sometimes reaching the size of those of *O. muricata,* but deeper yellow. The stigma is surrounded by the anthers which open early in the bud. The *velutina* and *laeta* which it produces from *Lamarckiana* can hardly be distinguished from those produced by the European *O. biennis*, although the leaves are narrower and darker green. I cultivated this strain during three succeeding generations.

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[3] *Oen. Hookeri* T. and G. = *Onagra Hookeri* Small = *O. biennis hirsutissima* Gray, Bot. Calif. See H. M. HALL, A botanical survey of San Jacinto Mountain. Univ. Calif. Publ. Bot. 1:98. 1902.

O. scintillans and *O. lata* are the mutant species described in my *Mutations-Theorie*. The *scintillans* used originated from *Lamarckiana* seed of 1889 which was sown in 1895. In 1906 I had the fourth generation from continued pure self-fertilizations and used it for my cross. From this same strain the *lata* used in the experiments of this article arose as a mutant in 1901. It was artificially fertilized. My crosses were made with specimens of the second and third generation of its progeny.

I will now describe the crosses from which the triplets resulted.

Oenothera scintillans × *strigosa*.—This cross was made in July, 1907, between two biennial specimens. It yielded a small lot of seed which was sown the next spring. From it arose 36 *laeta*, 21 *velutina*, 15 *scintillans*, and one *lata*, altogether 73 plants, most of which flowered during the summer. The *laeta* and *velutina* agreed with the description given above; the *lata* was a mutant. The *scintillans* were intermediate hybrids, which had the habit and leaves of the mother parent, or nearly so, but small flowers with the anthers surrounding and touching the stigma like the father. I fertilized all three forms with their own pollen and intend to sow the seed next year.

Oenothera lata × *strigosa*.—This cross was effected in 1905, both parents being annual specimens. I used different plants of *lata* and sowed the seed of one cross in 1906, of another cross in 1907, and a third lot in 1908. I got the following results:

Year	Number of specimens	Percentage *laeta*	Percentage *velutina*	Percentage *lata*
1906	41	36	59	5
1907	47	49	40	11
1908	270	27	34	38
Total	358	40	33	27

The *laeta* and *velutina* were the same as those from the cross with *Lamarckiana*. I sowed self-fertilized seed from plants of 1906 in 1907; the mothers were *velutina* and gave 113 children, most of which flowered. All of them were *velutina*. In 1907 I self-pollinated some *laeta* and some *velutina* and got 80 and 45 seedlings respectively. The first were all *laeta*, the second lot was uniformly *velutina*. Of each lot 25 specimens were preserved after the sorting period and observed during the time of flowering and ripening of their fruits.

The *lata* were intermediate between *O. lata* and *O. strigosa*. In 1908 I cultivated one half of them in the open and the other under an open glass-covering, both of them with cultures of ordinary *lata* under the same conditions for comparison. The *lata* from the *strigosa* cross had narrower leaves but with the rounded tips; the bracts were broad but less bent downward. The flowers were much smaller than those of the mother, but somewhat larger than those of the father. Their shape resembled that of *O. strigosa*, but the stigma showed, although in a lessened degree, the peculiar hand-shaped form of the ordinary *O. lata*. The anthers touched the stigma, but only with their lower halves. The flower buds were broad, and the tube was relatively short. In all these points and in the other characters the *lata* hybrids were strikingly intermediate between the two parents. Even the bent tips of the young leaves were to be seen, and at once revealed the father. But the most interesting feature was that of the pollen. *O. lata* is purely female, while *O. strigosa* has the ordinary supply of pollen. The hybrids showed some pollen and a relatively small number of fertile grains. These were, during ordinary weather, insufficient for fertilization, even if the pollen of many flowers was brought upon one stigma. But there were individual fluctuations, and so I succeeded in getting self-fertilized fruits on at least one specimen.

Oenothera lata × *O. biennis Chicago*.—This cross was made in 1905, both parents being annual. Two specimens of *O. lata* were used. I sowed their seed in different lots in the three succeeding years and had the following results:

Year	Number of specimens	Percentage *laeta*	Percentage *velutina*	Percentage *lata*
1906	33	27	70	3
1907	78	34	29	37
1908	167	36	28	35
Total	278	35	34	31

The *laeta* and the *velutina* were of the description already given. I sowed the self-fertilized seed of 1906 in 1907 and 1908 and had four lots of the second generation. The lots of the first included 69 and 139 individuals, all of which were *laeta;* the sowings of the other strain extended over 38 and 158 samples, all of which were *velutina.* Both of the twins thus complied with the rule of constancy in the second generation. From the lots of 1907 I cultivated in 1908 a third generation comprising 70 children of *laeta* and 90 of *velutina;* both lots were once more uniform and similar to their parents.

The *lata* individuals of this cross were almost similar to those of *O. lata* itself. However, they had the smaller flowers of *O. biennis,* with the self-fertilizing position of the stigma, and the long lobes of the father. Their flower buds were intermediate between those of the two parents. In 1906 and 1907 the anthers seemed wholly barren; but in 1908, during the very warm last days of July, they yielded some pollen, which was used partly for self-fertilization, partly for crosses.

O. lata × *Hookeri.*—This cross is the most interesting of all the crosses with *O. lata,* since its *lata* hybrids are almost as rich in pollen as any other evening primrose. This enabled me to study the second generation of the *lata,* which, in contrast to that of the *laeta* and the *velutina,* repeats the splitting. The yield of the pollen was small in the unfavorable summer of 1907, but large during the hot days of July and August, 1908.

I have made this cross twice, in 1905 and 1907; the parents were annual specimens. I had the following results in the first generation:

Year	Seed of	Number of specimens	Percentage *laeta*	Percentage *velutina*	Percentage *lata*
1907....................	1905	51	53	39	8
1908....................	1905	229	45	47	8
1908....................	1907	72	49	28	22
Total..............		352	47	42	11

Here also the *laeta* and *velutina* were the same as those from the cross with *Lamarckiana.* I sowed some self-fertilized seed of the *velutina* of 1906, partly in 1907 and partly in 1908, and cultivated from each lot 60 specimens, all of which repeated the *velutina* characters.

The *lata* specimens also were cultivated from seed of 1906 in both succeeding years. Their flowers were as large as those of both parents and intermediate in the tinge of the yellow, the *Hookeri* being paler yellow than the *Lamarckiana* and its *lata*. The anthers did not reach the stigma, which was often hand-shaped. The spike was much denser than that of *Hookeri* but thinner than that of the mother. Stem, veins, and calyx were reddish; and leaves were narrower than in *O. lata*. In all these and in other characters the plants were strikingly *lata*, but with the addition of the differentiating marks of the *Hookeri*.

The self-fertilized seed of the *lata* plants of the first generation gave a mixed progeny, consisting of *velutina* and *lata*, both resembling the types of the first year. No *laeta* specimens were produced. The numbers were the following:

Year	Number of seedlings	Percentage *velutina*	Percentage *lata*
1907	53	85	15
1908	134	81	19
Total	187	82	18

From the experiments described the following table may be compiled:

TRIPLE HYBRIDS AND THEIR SUCCEEDING GENERATIONS

Mother	Father	First generation Percentage	Second generation	Third generation
O. scintillans	× O. strigosa	49 laeta		
		29 velutina		
		21 scintillans		
O. lata	× O. strigosa	40 laeta	80 laeta	
		33 velutina	158 velutina	
		27 lata		
O. lata	× O. bien. Chicago	35 laeta	208 laeta	70 laeta
		34 velutina	196 velutina	90 velutina
		31 lata		
O. lata	× O. Hookeri	47 laeta		
		42 velutina	120 velutina	
		11 lata	82 per cent. velutina 18 per cent. lata	

QUADRUPLE HYBRIDS.—The discovery of twin and triple hybrids naturally suggests the idea of the possibility of a hybrid quartette. As a matter of fact the experiments did the same. In the case of *O. lata* × *O. biennis* from Chicago a fourth type appeared in one specimen, and in that of *O. lata* × *O. Hookeri* in two specimens. These three plants belonged evidently to the *lata* type, but combined with this the smooth, broad, and bright-green leaves of the *laeta*, whereas all the other *latas* of these crosses had gray and furrow-shaped leaves like the *velutina*. The *lata-laeta* of the first cross was sufficiently fertile, but of two of the *Hookeri* cross one had barren anthers and the other only some spare pollen in comparison with the rich supply of pollen in the other *lata* plants of this cross. In this respect, therefore, they also showed the character of the *laeta* type.

It would seem probable that the *lata-laeta* should be produced in the same number as the other *lata*, or *lata-velutina* as we could now call it. But then the *laeta* itself often appears in too small numbers. The cause of this phenomenon has still to be investigated.

Summary

1. Triple hybrids are produced in crosses of *Oenothera scintillans* and *O. lata* by such species as produce twins from *O. Lamarckiana*.

2. The species investigated are *O. strigosa* Rydb., *O. Hookeri* T. and G., and one of the American subspecies of *O. biennis*.

3. Of the triple hybrids, two are the same as the twins from the corresponding *Lamarckiana* crosses and bear the characters of *O. laeta* and *O. velutina* combined with those of the other parent.

4. The third type resembles the mother (*O. lata* or *O. scintillans*), but in its special marks is also intermediate between its parents.

5. The *laeta* and *velutina* are constant and uniform in their succeeding generations, so far as experience goes. In this respect they follow the rule for the twin hybrids of *O. Lamarckiana*.

6. The *lata*, however, in the only case tried, repeated the splitting after self-fertilization, producing, however, only *lata* and *velutina*.

7. It seems probable that the whole progeny of the crosses named should split up into two equal parts, *laeta* and *velutina*, and that each of them should produce a certain percentage of *lata*. In this way quadruple hybrids would arise.

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